Seasonal variation and an “outbreak” of frog predation by tamarins

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Abstract

We report temporal variation and an "outbreak" of frog predation by moustached tamarins, *Saguinus mystax*, in north-eastern Peruvian Amazonia. Frog predation rates were generally very low, but strongly increased in October 2015. Other high rates, identified by outlier analyses, were also observed in September, October or November of other years. Over all study years, predation rates in this three month period were significantly higher than those in the remainder of the year, suggesting a seasonal pattern of frog predation by tamarins. Reduced fruit availability or increased frog abundance or a combination of both may be responsible for both the seasonal pattern and the specific "outbreak" of frog predation.

Key words: Callitrichidae; *Saguinus mystax*; Hylidae; *Osteocephalus*; *Phyllomedusa*

Introduction

Predation on vertebrates has been reported for many primate species (Butynski 1982). The proportion of vertebrates in primate diets varies between species, but is generally low (Butynski, 1982). It may also vary between populations, groups or age-sex classes (Chapman and Fedigan 1990; Heymann et al. 2000; Pruetz 2006). In white-headed capuchin monkeys (*Cebus capucinus*), baboons (*Papio* spp.) and chimpanzees (*Pan troglodytes*), the consumption of vertebrate meat has strong social implications, through competition, collaborative or cooperative hunting, sharing of kills and hunting "binges" (Rose 1997; Newton-Fisher 2015; Sommer et al. 2016). Finally, predation on vertebrates can be highly seasonal, particularly in chimpanzees (Stanford et al., 1994; Mitani and Watts 2005).

Tamarins, New World monkey of the genera *Saguinus* and *Leontocebus*, prey on frogs and lizards, and occasionally consume bird eggs and nestlings (Neyman 1977; Terborgh 1983; Soini 1987; Peres 1993; Heymann et al., 2000). As with other primates, the proportion of vertebrates in the diet of *Saguinus* and *Leontocebus* is generally very low, accounting for 1%

or less of the overall diet (Castro Coronado 1991; Peres, 1993; Heymann et al., 2000; Porter 2001). In sympatric tamarins (*Saguinus mystax*/*Leontocebus nigrifrons* and *Saguinus imperator*/ *Leontocebus weddelli*), *Saguinus* mainly preys on arboreal frogs, *Leontocebus* mainly on trunk-living and terrestrial lizards (Terborgh, 1983; Heymann et al., 2000; but see Porter [2001] for *Saguinus labiatus*/*Leontocebus weddelli*), in line with their vertical niche segregation (Heymann and Buchanan-Smith 2000). Frogs and lizards are highly attractive resources; their capture usually results in other group members, not only infants and juveniles, approaching the successful hunter and begging or trying to steal the prey (personal observations) making vertebrate predation a very conspicuous event.

During behavioural data collection on a mixed-species group of *S. mystax* and *L. nigrifrons* at the Estación Biológica Quebrada Blanco (EBQB) between September and November 2015, we observed frog predation by *S. mystax* much more frequently than during any previous study. Therefore, we compiled data on frog predation from studies conducted at EBQB since 1985 to examine whether frog predation in October 2015 was in fact higher than during other periods, and if so, to explore potential causes of the increase. Furthermore, since the abundance of Neotropical frogs varies seasonally (Allmon 1991; Watling and Donnelly 2002) we asked whether there is a seasonal pattern of frog predation by *S. mystax*.

Methods

Study area

Ecology and behaviour of tamarins are studied at EBQB in north-eastern Peruvian Amazonia (4°21'S 73°09'W) by EWH and his students and collaborators since 1985. The EBQB study area mainly consists of primary tropical rainforest of the tierra firme type ("bosque de altura" following (Encarnación 1985), interspersed with small swampy areas ("bajiales"). The home range of one tamarin study group also includes ca. 4-5 ha of secondary forest (previous buffalo pasture regenerating since 2000) and a land strip close to Quebrada Blanco that can be inundated for a few days during the height of the rainy season. The area shows a strongly seasonal pattern of rainfall, with <200 mm of rain in the months of July, August and September (Supplementary Material 1: Figure S1).

Study group and observation methods

At EBQB, moustached tamarins, *S. mystax*, live in groups of 3-13 individuals and form mixed-species groups with black-fronted tamarins (Heymann & Buchanan-Smith 2000; Löttker et al. 2004; see group size information provided in the Supplementary Material 2). They are well habituated and depending on their height in the forest can be observed from less than 5 m distance. During research projects and field courses, groups are followed between 5 and 20 days per month (very rarely for fewer or more days). Data are collected with instantaneous scan sampling, focal animal sampling and behaviour sampling (Martin and Bateson 2007). The latter method is employed for rare but significant events, including predation by tamarins on vertebrates. Study periods and number of observation hours are provided in Supplementary Material 2. Whenever possible, photos are taken from predation events and prey residuals. Frogs were taxonomically identified using Medina Torres et al. (2012).

Data analyses

Data on frog predation are available since 1985 (Supplementary Material 2). From these data we calculated monthly predation rates as the number of predation events * individual^{-1} * 100 hours^{-1}; we considered only independently travelling individuals and used only data from months with at least three days of observation.

We performed a 1-way ANOVA with month as categorical and predation rate as dependent variable to analyse monthly variation of frog predation. Though variation was not significant, rates of September, October and November stuck out. Therefore, we used the Modified Thompson Tau Method (Cimbala 2011) for outlier identification to examine whether the rate observed in October 2015 and mean rates for September, October and November were exceptionally high (Supplementary Material 2). Additionally, we calculated the expected number of frog predation events for the periods September-November and December-August and compared these to the observed numbers with a Chi² test. Expected numbers per period were calculated as $Exp = N_{fpe} / N_{h\ obs} * N_{h\ obs\ p}$, where N_{fpe} is the total number of frog predation events, $N_{h\ obs}$ the total number of observation hours (7588.9) and $N_{h\ obs\ p}$ the number of observation hours per period. Finally, we compared frog predation rates between September-October and December-August with the Mann-Whitney U-test. ANOVA, Chi² test and Mann-Whitney U-test were performed in Statistica© 13 (Dell Inc. 2015).

Results

Monthly frog predation rates did not vary significantly ($F_{11,114} = 1.696$, $0.05 < p < 0.1$; Fig. 2). However, all outliers in the raw dataset came from September, October or November (Supplementary Material 2). Also, amongst all monthly means October (0.31) and November (0.32) and amongst monthly maxima October 2015 (1.70) were identified as outliers. The number of frog predation events observed in the period September-November was significantly higher than expected, based on the number of observation hours for these months ($Chi^2 = 40.849$, $df = 1$, $p < 0.001$; Supplementary Material 1). Also, monthly frog predation rates were significantly higher for the period September-November compared to December-August (Mann-Whitney U-test, $Z = 3.141$, $p < 0.005$; $N_{Sep\text{-}Nov} = 45$ months, $N_{Dec\text{-}Aug} = 80$ months).

Frogs for which taxonomic identification was possible belonged to the genera *Osteocephalus* (n=9; Fig. 3), *Phyllomedusa* (n=5) and *Hyla* (n=1) from the family Hylidae and were greenish, beige/greyish or brown. Judging from coloration and size, members of these genera also were the prey eaten in many other cases. Except for one case, all captures took place in trees. In one case, several tamarins climbed down to the forest floor and intensively watched the edge of a small pond. After ca. 10 min, one tamarin reached into the water and pulled out a frog and started to feed on it. The frog had probably dropped from the tree, an escape strategy observed on several opportunities.

Discussion

In our study area, fruit availability is lower between the late rainy season (May/June) and the onset of the rainy season (October/November; Supplementary Material: Fig. S2). Therefore, increased frog predation between September and November cannot simply be explained as a compensation of reduced fruit availability. It is more likely that availability of frogs plays a role. Neotropical rainforest frogs show strong seasonal variation in activity and reproduction. Frog abundance peaks in the rainy season in Amazonia, but may vary between years (Allmon 1991; Duellman 2005). The high variance of frog predation rates, particularly between September and November (Fig. 2) and the 2015 "outbreak" could relate to such inter-annual variation.

Precipitation is a trigger for increased activity and the onset of reproduction of tropical frogs (Donnelly and Guyer 1994; Blaustein et al. 2010). Some species like *Osteocephalus taurinus* show explosive breeding at the beginning of the rainy season (Duellman, 2005). Also, frog activity may correlate with peaks of heavy rainfall rather than total precipitation during a given period (Duellman 1995). Although September 2015 was drier than average (84 mm vs. 183 mm, 95% CI 144-223 mm), there were several short but heavy rains in late September before the first frog predation was observed. This would be in line with the trigger function of precipitation quoted above.

The frog genera preyed upon by *S. mystax* are all arboreal and nocturnal (Duellman 2005; Menin et al. 2008). Predation on these frogs by *S. mystax* fits with the prey foraging of this tamarin species in the lower canopy, mainly between ca. 8 and 15 m (Heymann & Buchanan-Smith, 2000). *Saguinus mystax* mainly detect and capture prey that is nocturnal and spends the day stationary in one place, relying on cryptic or inconspicuous coloration (Nickle and Heymann 1996; Smith 2000). At EBQB, *Osteocephalus* was the most abundant anuran genus in a survey in October-December 2016 (Schulz 2017). This supports the notion that frog abundance may play a role for the observed temporal patterns. In the absence of long-term data on frog availability a more definite conclusion cannot be drawn. In any case, our results support the notion that vertebrate predation by primates can be seasonal.

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Legends to figures

Fig. 1 Monthly pattern of frog predation by *Saguinus mystax*. Means (●) ± 95% confidence intervals (whiskers)

Fig. 2 (a) *Saguinus mystax* preying on an *Osteocephalus taurinus* (Photo: Eckhard W. Heymann). (b) An *Osteocephalus* sp. dropped by a *S. mystax* after consumption of the hind legs (Photo: Marieke Wübker)

Figure 2

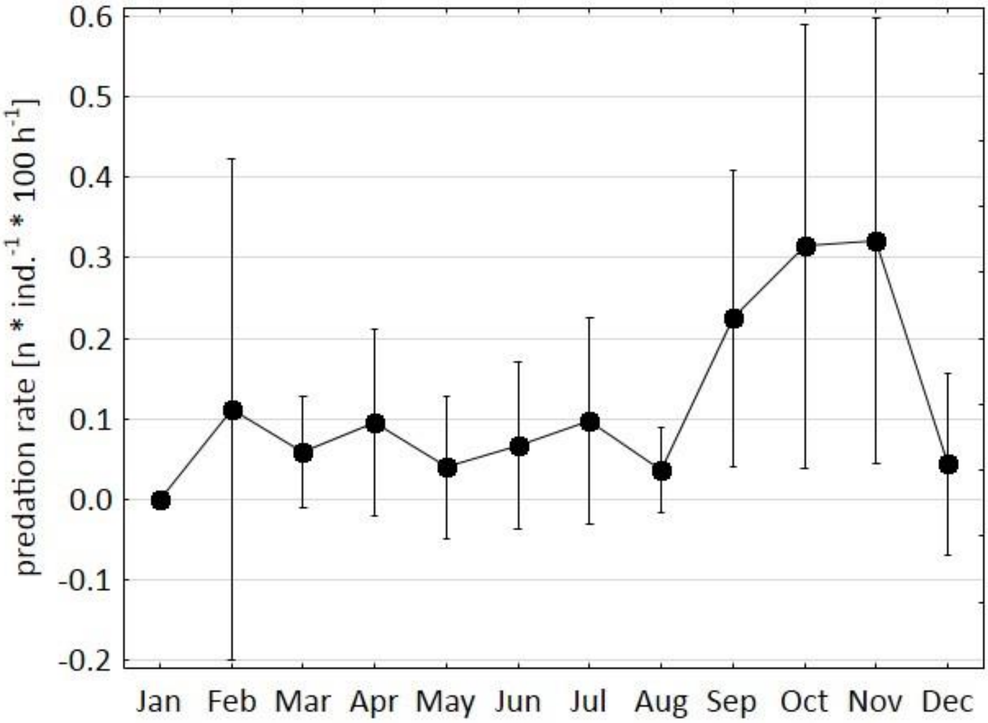
predation rate [n * ind.$^{-1}$ * 100 h^{-1}]
0.6
0.5
0.4
0.3
0.2
0.1
0.0
-0.1
-0.2
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec

Figure 2a

Figure 2b

Lueffe et al.: Supplementary Material 1

<u>Rainfall</u>

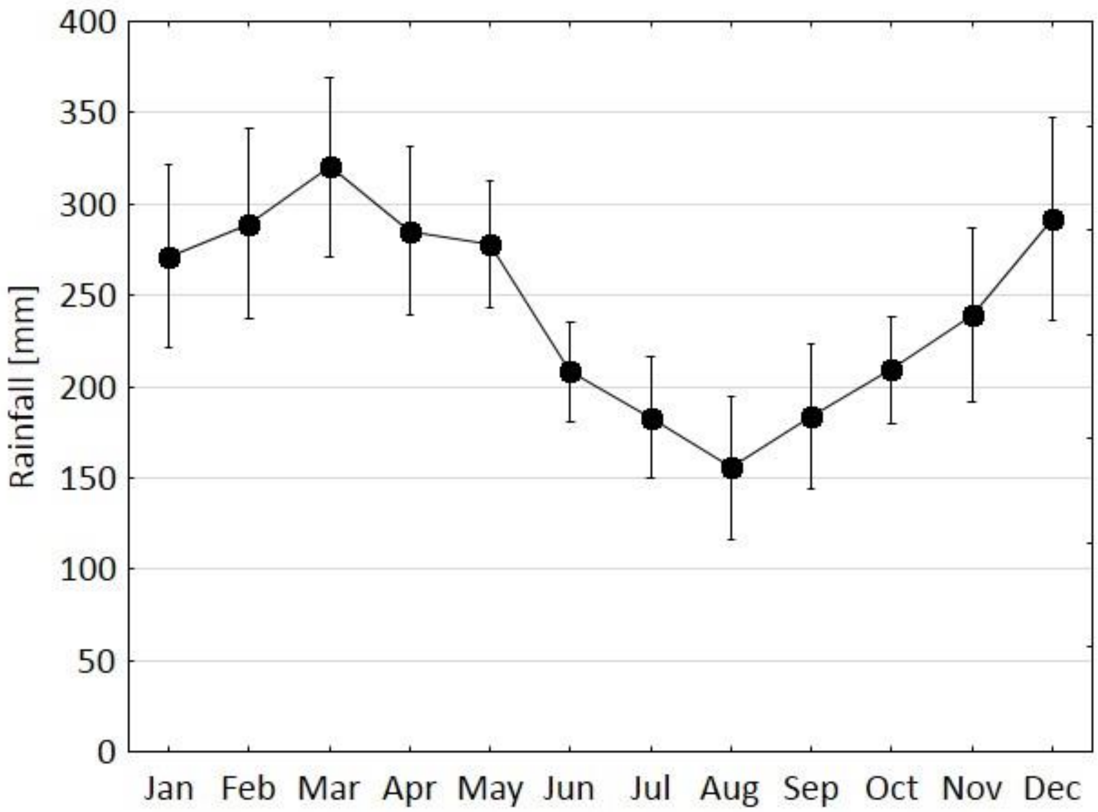

Fig S1 Monthly variation of rainfall at Tamshiyacu (4°00’10.7”S 73°09’38.2”W), ca. 40 km north of EBQB, between 1997 and 2016. Means (●) ± 95% confidence intervals (whiskers). Raw data downloaded from http://www.senamhi.gob.pe

Fruiting phenology

In monthly phenological observations, the presence of ripe fruits was scored as present or absent, following Peres (1994). A monthly fruiting index was then calculated as the number of trees with ripe fruits present divided by the number of trees examined (n = 216). Fig. S3 is based on 5 years for which phenological data were available for at least 9 months.

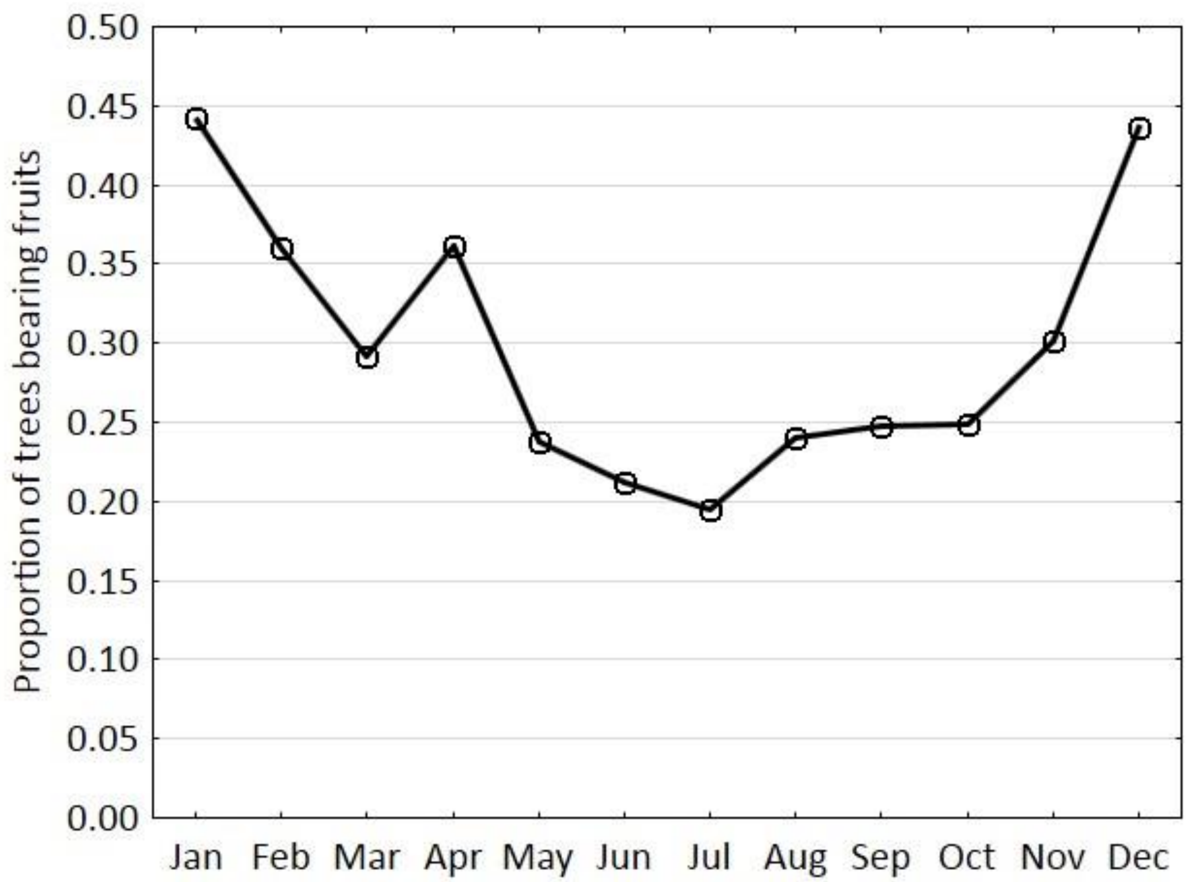

Fig S2 Fruiting phenology at EBQB.

Observed vs. expected numbers of frog predation events

Period	# of hours of observation	Observed # of frog predation events	Expected # of frog predation events
September-November	2534.8	46	22
December-August	5054.1	19	43

$Chi^2 = 40.849$, $df = 1$, $p < 0.001$

Reference for Supplementary Material

Peres CA (1994) Primate responses to phenological changes in an Amazonian terra firme forest. Biotropica 26:98-112

Lueffe et al.: Supplementary Material 1

This Excel file includes the database of the manuscript by Lüffe et al
on frog predation by moustached tamarins, *Saguinus mystax*
It also includes the outlier analyses performed with the method
by Cimbala (2011)

Year	Month	Group	Group size	# of hours of observation	# of predation events	Predation rate (PR)	abs(PR - mean of all PR)
1985	Jul	2	3	40.9	0	0.000	0.141
1985	Aug	2	3	57.0	0	0.000	0.141
1985	Sep	2	3	28.8	0	0.000	0.141
1985	Oct	2	3	26.5	0	0.000	0.141
1985	Nov	2	3	66.8	3	1.498	1.357
1986	Feb	2	3	29.2	0	0.000	0.141
1986	Mar	2	3	48.5	0	0.000	0.141
1986	Apr	2	3	64.7	0	0.000	0.141
1986	May	2	3	46.2	0	0.000	0.141
1990	Jun	2	5	44.3	0	0.000	0.141
1990	Jul	2	5	113.5	1	0.176	0.035
1990	Aug	2	4	121.8	1	0.205	0.064
1990	Sep	2	4	51.9	0	0.000	0.141
1994	Mar	1	4	35.0	0	0.000	0.141
1994	Apr	1	4	62.7	1	0.399	0.258
1994	May	1	4	69.8	0	0.000	0.141
1994	Jun	1	4	49.5	1	0.505	0.364
1994	Jul	1	4	42.3	0	0.000	0.141
1994	Aug	1	4	87.8	0	0.000	0.141
1994	Sep	1	4	33.7	1	0.742	0.601
1994	Oct	1	5	42.2	0	0.000	0.141
1994	Nov	1	4	90.0	0	0.000	0.141
1994	Dec	1	5	76.0	1	0.263	0.122
1995	Jan	1	5	41.0	0	0.000	0.141
1995	Feb	1	5	102.0	0	0.000	0.141
1995	Mar	1	4	111.0	1	0.225	0.084
1995	Apr	1	3	109.0	0	0.000	0.141
1995	May	1	3	126.0	0	0.000	0.141
1995	Jun	1	3	116.0	0	0.000	0.141
1995	Jul	1	5	106.0	0	0.000	0.141
1995	Aug	1	5	141.0	0	0.000	0.141
1995	Sep	1	5	68.0	0	0.000	0.141
1995	Oct	1	5	63.0	1	0.317	0.176
1995	Nov	1	5	51.0	1	0.392	0.251
1997	Mar	1	8	27.3	0	0.000	0.141
1997	Apr	1	8	56.8	1	0.220	0.079
1997	May	1	8	38.0	0	0.000	0.141
1997	Jun	1	8	33.0	0	0.000	0.141
1997	Jul	1	8	47.2	2	0.530	0.388
1997	Aug	1	8	64.7	0	0.000	0.141
1997	Sep	1	8	28.0	0	0.000	0.141
1997	Oct	1	8	25.8	0	0.000	0.141

1997	Nov	1	8	39.2	0	0.000	0.141
1997	Dec	1	8	39.3	0	0.000	0.141
1998	Feb	1	8	37.3	0	0.000	0.141
1998	Mar	1	8	38.8	0	0.000	0.141
1998	Apr	1	8	29.3	0	0.000	0.141
1998	May	1	8	26.0	0	0.000	0.141
1998	Jun	1	8	26.7	0	0.000	0.141
1998	Jul	1	8	52.6	0	0.000	0.141
1998	Aug	1	8	26.7	0	0.000	0.141
1998	Sep	1	8	37.7	0	0.000	0.141
1998	Oct	1	8	27.8	0	0.000	0.141
1998	Nov	1	8	33.1	0	0.000	0.141
2000	Jan	1	5	126.0	0	0.000	0.141
2000	Feb	1	5	137.0	0	0.000	0.141
2000	Mar	1	5	136.0	1	0.147	0.006
2000	Apr	1	5	139.0	0	0.000	0.141
2000	May	1	5	120.0	0	0.000	0.141
2000	Jun	1	5	135.0	2	0.296	0.155
2000	Jul	1	5	74.0	1	0.270	0.129
2000	Aug	1	5	84.0	0	0.000	0.141
2000	Sep	1	5	57.0	0	0.000	0.141
2000	Oct	1	5	78.0	0	0.000	0.141
2000	Nov	1	5	81.0	1	0.247	0.106
2000	Dec	1	5	55.0	0	0.000	0.141
2000	Jul	2	8	61.0	0	0.000	0.141
2000	Aug	2	8	59.0	0	0.000	0.141
2000	Sep	2	8	64.0	0	0.000	0.141
2000	Oct	2	8	61.0	0	0.000	0.141
2000	Dec	2	8	61.0	0	0.000	0.141
2002	Oct	1	3	25.5	0	0.000	0.141
2002	Nov	1	3	26.3	0	0.000	0.141
2002	Aug	2	8	45.4	0	0.000	0.141
2002	Sep	2	8	56.1	1	0.223	0.082
2002	Nov	2	6	28.6	1	0.583	0.442
2002	Dec	2	6	27.2	0	0.000	0.141
2002	Aug	3	5	29.4	0	0.000	0.141
2002	Sep	3	5	28.9	0	0.000	0.141
2002	Oct	3	5	30.2	2	1.325	1.183
2002	Nov	3	5	23.8	0	0.000	0.141
2002	Dec	3	5	26.4	0	0.000	0.141
2003	May	1	4	30.1	0	0.000	0.141
2003	Jun	1	4	23.6	0	0.000	0.141
2003	Jul	1	4	23.8	0	0.000	0.141
2003	Jan	2	6	29.4	0	0.000	0.141
2003	Feb	2	6	29.7	1	0.561	0.420
2003	Mar	2	6	26.5	0	0.000	0.141

2003	May	2	4	30.3	0	0.000	0.141
2003	Jun	2	4	31.0	0	0.000	0.141
2003	Aug	2	4	28.4	0	0.000	0.141
2003	Jan	3	6	26.7	0	0.000	0.141
2003	Jun	3	6	24.1	0	0.000	0.141
2003	Aug	3	6	26.6	0	0.000	0.141
2004	Aug	1	7	38.5	0	0.000	0.141
2004	Sep	1	7	38.5	1	0.371	0.230
2004	Oct	1	7	38.5	3	1.113	0.972
2005	Mar	1	6	38.5	0	0.000	0.141
2005	Apr	1	6	38.5	0	0.000	0.141
2005	May	1	6	38.5	1	0.433	0.292
2009	Mar	1	6	77.4	1	0.215	0.074
2009	Apr	1	6	68.9	1	0.242	0.101
2009	May	1	6	46.9	0	0.000	0.141
2009	Jun	1	6	53.1	0	0.000	0.141
2009	Mar	3	7	76.9	0	0.000	0.141
2009	Apr	3	7	69.1	0	0.000	0.141
2009	May	3	7	41.9	0	0.000	0.141
2009	Jun	3	7	52.1	0	0.000	0.141
2010	Sep	1	5	67.7	1	0.295	0.154
2010	Oct	1	5	42.3	1	0.473	0.332
2012	Nov	1	6	56.5	0	0.000	0.141
2013	Oct	1	11	100.0	0	0.000	0.141
2014	Oct	1	13	90.0	3	0.256	0.115
2015	Sep	1	8	40.5	3	0.926	0.785
2015	Oct	1	8	81.0	11	1.698	1.556
2015	Nov	1	8	48.6	3	0.772	0.630
2016	Oct	1	6	105.0	1	0.159	0.018
2016	Nov	1	6	121.0	5	0.689	0.548
2016	Oct	2	13	83.8	0	0.000	0.141
2016	Nov	2	13	142.0	0	0.000	0.141
2017	Jun	1	6	134.6	0	0.000	0.141
2017	Jul	1	6	135.2	0	0.000	0.141
2017	Aug	1	6	113.7	2	0.293	0.152
2017	Sep	1	6	85.1	3	0.588	0.446
2017	Oct	1	6	120.4	0	0.000	0.141

TINV	1.946	TINV from Table in Cimbala 2011
tau	1.909	
mean	0.141	
SD	0.305	
tau * SD	0.582	
		identified outliers

Month	Mean monthly PR	abs(Mean monthly PR - mean of all monthly PR)		
Jan	0.000	0.120	TINV	2.179
Feb	0.094	0.026		
Mar	0.053	0.066	tau	1.802
Apr	0.096	0.024		
May	0.096	0.023	mean	0.120
Jun	0.067	0.053	SD	0.108
Jul	0.098	0.022		
Aug	0.036	0.084	tau * SD	0.194
Sep	0.225	0.105		
Oct	0.314	0.194		
Nov	0.322	0.202		
Dec	0.038	0.082		

TINV from Table in Cimbala 2011

identified outliers

Month	Maximum monthly PR	abs(Maximum monthly PR - mean of all maxima)
Jan	0.000	0.635
Feb	0.561	0.074
Mar	0.225	0.410
Apr	0.399	0.236
May	0.723	0.088
Jun	0.505	0.130
Jul	0.530	0.105
Aug	0.293	0.342
Sep	0.926	0.291
Oct	1.698	1.063
Nov	1.498	0.863
Dec	0.263	0.372

TINV	2.179
tau	1.802
mean	0.635
SD	0.512
tau * SD	0.922

TINV from Table in Cimbala 2011

identified outliers